

# SOME FLORAL NECTAR-SUGAR COMPOSITIONS OF SPECIES FROM SOUTHEASTERN ARIZONA AND SOUTHWESTERN NEW MEXICO

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## ABSTRACT

The floral nectar-sugar compositions of 34 species from southeastern Arizona and southwestern New Mexico were determined by high-performance liquid chromatography (HPLC). Of these, 26 species have not been reported previously. Among the species surveyed were hummingbird flowers (18 species), hawkmoth flowers (seven species), bee flowers of various kinds (five species), butterfly flowers (two species), and those whose pollinators were not known (two species). Both the hummingbird and hawkmoth nectars were high in sucrose, averaging 71% and 81% respectively. The nectars of the purportedly butterfly flowers were very different at 76% and 46% sucrose. Bee nectars from large-flowered species with large corolla tube openings were high in sucrose (average = 76%) whereas small-flowered bee species with small corolla tube openings were lower in sucrose (average = 35%).

It is clear from the work of Baker (1978) and Baker and Baker (1975, 1979, 1983) that the sugar composition of floral nectars is worthy of careful examination in regard to its differential attractiveness to various groups of potential pollinators. It has been found that the most common sugars in nectars are the hexoses, glucose and fructose, and the disaccharide sucrose. These are the so-called "big three" sugars of nectars (Baker and Baker 1983). Other sugars are occasionally present in very small amounts.

We present here the floral nectar-sugar compositions of a series of species from southeastern Arizona and southwestern New Mexico. The pollinators of many of these species have been studied but their sugar compositions have not been reported.

## METHODS AND MATERIALS

Sugar compositions by mass were quantified using HPLC. The methods employed are described in earlier publications (Freeman et al. 1983, Freeman et al. 1984). HPLC was used because the analysis is direct, eliminating the derivatization steps of other techniques that add to the error term. This makes HPLC much more accurate. In addition, HPLC is much more rapid. Sugar compositions were calculated to the nearest 0.1%. Voucher specimens are deposited at UTEP. Nomenclature follows Lehr (1978) and Lehr and Pinkava (1980).

## RESULTS AND DISCUSSION

The nectar-sugar compositions of 34 species are presented in Table 1. Freeman et al. (1984) have previously reported on seven species (*Bouvardia glaberrima*, *Epilobium canum* subsp. *latifolia* [as *Zauschneria latifolia*], *Fouquieria splendens*, *Mimulus cardinalis*, *Penstemon barbatus*, *P. pseudospectabilis*, and *Silene laciniata*). Sherbrooke and Schereens (1979) have reported on *Erythrina flabelliformis*. About half of the species surveyed in this study are known or suspected to be hummingbird-pollinated. These include *Anisacanthus thurberi*, *Aquilegia triternata*, *Bouvardia glaberrima*, *Castilleja patriotica*, *Erythrina flabelliformis*, *Fouquieria splendens*, *Lonicera arizonica*, *Lobelia cardinalis*, *Mimulus cardinalis*, *Penstemon barbatus*, *P. pinifolius*, *P. pseudospectabilis*, *Ribes pinetorum*, *Salvia lemmoni*, *Silene laciniata*, and *Epilobium canum* subsp. *latifolium*. These nectars ranges in sucrose composition from 55% (*Mimulus cardinalis*) to 93% (*Ribes pinetorum*).

The mean value of 71% sucrose is very similar to the means of other groups of hummingbird flowers (Freeman et al. 1984, Freeman, unpubl. data). In addition, many of these species also have a hexose imbalance; i.e., fructose is present in much larger quantities than glucose. A reversed imbalance is found in *Aquilegia triternata*, which has about twice as much glucose as fructose. In this species hexoses are present in very low quantities. The sugar composition of the floral nectar of *Erythrina flabelliformis* collected in this study from the Dragoon Mountains of Arizona is virtually identical with a sample collected and analyzed earlier from the same mountain range (Sherbrooke and Schereens 1979) also using HPLC as the analysis technique. Several species previously reported by Freeman et al. (1984) from other localities had very similar sugar compositions in the study area, including *Bouvardia glaberrima*, *Penstemon barbatus*, and *P. pseudospectabilis*. Others varied somewhat. The sucrose composition of *Silene laciniata* in the Chiricahua Mountains averaged about 10% higher than a sample of the same species from the White Mountains, also in eastern Arizona. *Mimulus cardinalis* and *Epilobium canum* subsp. *latifolium* nectars, however, were lower in sucrose in southeastern Arizona (Freeman et al. 1984). *Lonicera arizonica* was very similar in sugar composition to a sample of *L. involucreata*, also hummingbird-pollinated, reported previously (Freeman et al. 1984).

Brown and Kodrick-Brown (1979) report a population of *Lobelia cardinalis* in the White Mountains of eastern Arizona that did not produce nectar. They suggested that this population was mimetic to several common hummingbird-pollinated species in the area. Other populations of that species in the Chiricahua Mountains in southeastern Arizona and near Montezuma Wells National Monument

TABLE 1. NECTAR SUGAR COMPOSITIONS FOR SPECIES FROM SOUTHEASTERN ARIZONA AND SOUTHWESTERN NEW MEXICO. N = number of determinations.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
HUMMINGBIRD				
<i>Anisacanthus thurberi</i> (Torr.) Gray				
AZ, Santa Cruz Co., Pajarito Mtns.	2	17.7 ± 0.06	19.4 ± 1.6	63.0 ± 2.3
AZ, Santa Cruz Co., Pena Blanca Lake	3	12.1 ± 3.6	15.0 ± 2.9	72.9 ± 6.5
AZ, Cochise Co., Dragoon Mtns.	6	15.7 ± 2.3	15.1 ± 3.7	69.2 ± 5.7
Total =	11	15.1 ± 3.1	15.8 ± 3.4	69.1 ± 6.1
<i>Aquilegia triternata</i> Payson				
AZ, Cochise Co., Chiricahua Mtns.	2	3.1 ± 0.7	8.4 ± 5.6	88.6 ± 6.3
<i>Bouvardia glaberrima</i> Engelm.				
AZ, Cochise Co., Chiricahua Mtns.	6	33.4 ± 1.6	10.0 ± 1.8	56.7 ± 2.8
<i>Castilleja integra</i> Gray				
NM, Luna Co., Florida Mtns.	3	19.1 ± 4.2	5.8 ± 1.1	75.1 ± 4.0
<i>Castilleja pat riotica</i> Fern.				
AZ, Cochise Co., Chiricahua Mtns.	1	15.2	3.3	81.5
<i>Epilobium canum</i> (Greene) subsp. <i>latifolia</i> (Hook.) Raven				
AZ, Cochise Co., Chiricahua Mtns.	3	19.2 ± 3.2	18.6 ± 4.0	62.3 ± 7.0
<i>Erythrina flabelliformis</i> Kearney				
AZ, Cochise Co., Dragoon Mtns.	7	20.2 ± 3.6	19.5 ± 5.1	60.3 ± 6.1

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
<i>Fouquieria splendens</i> Engelm. NM, Hidalgo Co., Peloncillo Mtns.	1	18.4	16.6	65.0
<i>Lobelia cardinalis</i> L. AZ, Cochise Co., Huachuca Mtns.	6	28.8 ± 1.6	13.8 ± 1.0	57.2 ± 1.9
<i>Lonicera arizonica</i> Rehd. NM, Grant Co., Pinos Altos Mtns.	4	10.7 ± 5.9	14.6 ± 14.6	74.7 ± 13.1
<i>Mimulus cardinalis</i> Dougl. AZ, Cochise Co., Chiricahua Mtns.	1	34.6	10.1	55.3
<i>Penstemon barbatus</i> (Cav.) Roth. AZ, Cochise Co., Chiricahua Mtns.	37	12.1 ± 5.0	13.4 ± 5.4	74.5 ± 10.3
<i>Penstemon pinifolius</i> Greene AZ, Cochise Co., Chiricahua Mtns.	5	16.9 ± 2.6	19.2 ± 3.3	68.8 ± 5.7
<i>Penstemon pseudospectabilis</i> Jones AZ, Cochise Co., Chiricahua Mtns.	32	15.0 ± 4.3	19.0 ± 5.0	66.1 ± 9.2
<i>Penstemon ramosus</i> Crosswhite NM, Hidalgo Co., Peloncillo Mtns.	7	19.2 ± 3.9	22.4 ± 3.6	58.4 ± 7.5
<i>Ribes pinetorum</i> Greene AZ, Cochise Co., Chiricahua Mtns.	4	5.8 ± 0.9	0.7 ± 0.3	93.5 ± 1.1
<i>Salvia lemmonii</i> Gray AZ, Cochise Co., Chiricahua Mtns.	5	7.9 ± 1.6	4.0 ± 1.2	88.3 ± 2.4

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
<i>Silene laciniata</i> Cav. AZ, Cochise Co., Chiricahua Mtns.	3	14.1 ± 0.9	4.1 ± 0.7	81.8 ± 0.5
Mean		17.2 ± 8.5	12.1 ± 6.7	71.0 ± 12.0
HAWKMOOTH				
<i>Aquilegia chrysantha</i> Gray AZ, Cochise Co., Chiricahua Mtns.	1	4.2	9.0	86.8
AZ, Apache Co., White Mtns.	1	2.0	3.0	95.0
<i>Calylophus hartwegii</i> (Benth.) Raven NM, Hidalgo Co., Peloncillo Mtns.	1	5.5	4.1	90.4
<i>Castilleja sessiliflora</i> Pursh AZ, Santa Cruz Co., Mustang Mtns.	3	17.3 ± 1.5	7.0 ± 0.4	75.7 ± 1.9
<i>Datura meteloides</i> DC. AZ, Cochise Co., Huachuca Mtns.	1	11.1	9.6	79.3
<i>Ipomopsis longiflora</i> (Torr.) V. Grant AZ, Cochise Co., W. Jct. Hwys 82-90	1	11.5	11.4	77.2
<i>Ipomopsis thurberi</i> (Torr.) V. Grant AZ, Cochise Co., Huachuca Mtns.	7	16.0 ± 2.2	13.5 ± 2.9	70.6 ± 5.0
<i>Oenothera caespitosa</i> Nutt. NM, Luna Co., Florida Mtns.	1	6.0	4.1	89.9
Mean		10.1 ± 5.3	8.0 ± 3.6	82.0 ± 8.3

TABLE 1. CONTINUED.

Pollinator, Species Locality	N	% fructose ± s.d.	% glucose ± s.d.	% sucrose ± s.d.
<b>BEE</b>				
<i>Agave parviflora</i> Torr.				
AZ, Santa Cruz Co., Pena Blanca Lake	2	30.4 ± 0.1	29.1 ± 0.5	40.6 ± 0.6
<i>Penstemon dasyphyllus</i> Gray				
AZ, Cochise Co., Chiricahua Mtns.	7	30.0 ± 4.9	33.1 ± 6.6	38.3 ± 11.4
AZ, Santa Cruz Co., Mustang Mtns.	4	13.1 ± 3.8	16.3 ± 4.0	70.6 ± 7.7
<i>Penstemon linarioides</i> Gray				
NM, Grant Co., Silver City	2	32.7 ± 0.7	35.5 ± 0.4	31.7 ± 1.1
<i>Penstemon stenophyllus</i> Gray				
AZ, Cochise Co., Huachuca Mtns.	1	27.0	12.1	60.9
<i>Sweetia radiata</i> (Kell.) Kuntze				
NM, Grant Co., Pinos Altos Mtns.	1	38.3	31.6	30.1
Mean		28.6 ± 8.5	26.3 ± 9.7	45.4 ± 16.6
<b>BUTTERFLY</b>				
<i>Nyctaginea capitata</i> Choisy				
NM, Grant Co., Apache Mtns.	2	12.8 ± 2.3	11.2 ± 6.1	76.0 ± 8.4
<i>Ipomopsis macombii</i> (Torr.) V. Grant				
AZ, Cochise Co., Chiricahua Mtns.	3	26.1 ± 4.0	27.4 ± 4.5	46.4 ± 8.4
<b>UNKNOWN</b>				
<i>Hedeoma hyssopifolium</i> Gray				
AZ, Cochise Co., Chiricahua Mtns.	1	10.7	12.9	76.4
<i>Mertensia franciscana</i> Heller				
NM, Grant Co., Pinos Altos Mtns.	1	54.5	43.2	2.3



in central Arizona do produce nectar. We found a population of *L. cardinalis* in the Guadalupe Mountains of trans-Pecos Texas that also did not produce nectar, even when the plants were removed from the field and grown in a greenhouse. We found ample production of nectar in a population sampled in the Huachuca Mountains in this study, although the nectar was rather low in sucrose for a hummingbird flower (57%).

The hawkmoth-pollinated taxa sampled in this study include *Ipomopsis longiflora*, *I. thurberi* (Grant and Grant 1968), *Castilleja sessiliflora* (Cruden et al. 1983), *Datura meteloides* (Grant 1983, Grant and Grant 1983), *Aquilegia chrysantha* (Miller 1982), *Oenothera caespitosa* (Grant 1983), and presumably *Calylophus hartwegii* because of its great similarity to the other hawkmoth-pollinated *Oenothera* species (Cruden et al. 1983). All have the high-sucrose nectars described by Baker and Baker (1983) for this pollinator syndrome, averaging 81%. *Ipomopsis thurberi* has the lowest sucrose composition among this group and its overall composition is very similar to that of the closely related hummingbird taxon *I. aggregata* (Freeman et al. 1984, Freeman, unpubl. data), from which it differs only in color. *Castilleja sessiliflora* has a nectar-sugar composition like the other hummingbird-pollinated *Castilleja* species studied to date (Freeman et al., 1984, Freeman, unpubl. data).

Two of the three populations for which floral morphology suggests large-bee pollination had high-sucrose nectars. *Penstemon stenophyllus* and one population of a similar species, *P. dasyphyllus*, had 71% and 61% sucrose, respectively. In contrast, another population of *P. dasyphyllus* averaged only 38% sucrose. The reason for this difference in populations separated by only about 130 km and at the same latitude is not known. The smaller flowered *P. linarioides*, however, produces a nectar much lower in sucrose, and is perhaps pollinated by short-tongued bees, as its size and nectar-sugar composition suggest (Baker and Baker 1983). Schaffer and Schaffer (1977) studied nectar secretion and pollinators of four species of *Agave* from Arizona, of which three (*A. schottii*, *A. toumeyana*, and *A. parviflora*) are in subgenus *Littaea* and are probably closely related. While the three species vary in time of daily nectar secretion and sugar concentrations, all are pollinated by large bees (*Bombus sonorus* and *Xylocopa arizonensis*). *Agave parviflora*, reported here, has a nectar-sugar composition like those of *A. schottii* and *A. toumeyana*, which are atypical of the agaves surveyed to date (Freeman et al. 1983). The pollinators of *Swertia radiata* (or *Frasera speciosa*) have been studied in detail by Beattie et al. (1973). A wide variety of insects, primarily hymenopterans, dipterans, and lepidopterans, visited flowers of this species in Colorado. The nectar-sugar composition is very similar to the majority of the bee-pollinated taxa in this study.

Two purportedly butterfly-pollinated species, *Nyctaginea capitata* (Cruden et al. 1983) and *Ipomopsis macombii* (Grant and Grant 1965), were sampled. Baker and Baker (1983) have described butterfly nectars as being predominately either sucrose-rich or -dominated. *Nyctaginea capitata*, at 76% sucrose, fits that description. However, *I. macombii*, at an average of 46% sucrose, is considerably more hexose-rich. A study of butterfly and skipper nectars, utilizing more sensitive analytical techniques, is needed in order to more adequately define them statistically. Only then will it be possible to determine if either of these nectars is anomalous.

*Hedeoma hyssopifolium*, and *Mertensia franciscana* are coniferous forest species with unknown pollinators. *Hedeoma hyssopifolium* has the typical high-sucrose nectar of the family Lamiaceae (Baker and Baker 1983). The nectar of *Mertensia* is low in sucrose, which, along with open flowers, suggests pollination by short-tongued bees or flies.

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#### LITERATURE CITED

- BAKER, H. G. 1978. Chemical aspects of the pollination biology of woody plants in the tropics. In P. B. Tomlinson and M. H. Zimmerman, eds., *Tropical trees as living systems*, p. 57–82. Cambridge Univ. Press, Cambridge.
- and I. BAKER. 1975. Nectar constitution and pollinator-plant coevolution. In L. E. Gilbert and P. H. Raven, eds., *Animal and plant coevolution*, p. 100–140. Univ. of Texas Press, Austin.
- and ———. 1979. Sugar ratios in nectars. *Phytochem. Bull.* 12:43–45.
- and ———. 1982. Chemical constituents of nectar in relation to pollinator mechanisms and phylogeny. In M. N. Nitecki, ed., *Biochemical aspects of evolutionary biology*, p. 131–171. Univ. of Chicago Press, Chicago.
- and ———. 1983. Floral nectar sugar constituents in relation to pollinators. In C. E. Jones and R. J. Little, eds., *Handbook of experimental pollination biology*, p. 117–141. Van Nostrand-Reinhold Co., NY.
- BEATTIE, A. J., D. E. BREEDLOVE, and P. H. RAVEN. 1973. The ecology of the pollinators and predators of *Frasera speciosa*. *Ecology* 54:81–91.
- BROWN, J. H. and A. KODRICK-BROWN. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* 60: 1022–1035.
- , T. G. WHITHAM, and H. W. BOND. 1981. Competition between hummingbirds and insects for the nectar of two species of shrubs. *Southw. Naturalist* 26:133–145.
- CRUDEN, R. W., S. M. HERMANN, and S. PETERSON. 1983. Patterns of nectar production and plant-pollinator coevolution. In B. Bentley and T. Elias, eds., *The biology of nectaries*, p. 80–125. Columbia Univ. Press, NY.
- FREEMAN, C. E., W. H. REID, and J. E. BECVAR. 1983. Nectar sugar composition in some species of *Agave* (Agavaceae). *Madroño* 30:153–158.
- , ———, ———, and R. SCOGIN. 1984. Similarity and apparent convergence



- in the nectar-sugar composition of some hummingbird-pollinated flowers. Bot. Gaz. 145:132-135.
- GRANT, K. A. and V. GRANT. 1965. Flower pollination in the Phlox family. Columbia Univ. Press, NY.
- and ———. 1968. Hummingbirds and their flowers. Columbia Univ. Press, NY.
- GRANT, V. 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. Bot. Gaz. 144:439-449.
- and K. A. GRANT. 1983. Behavior of hawkmoths on flowers of *Datura meteloides*. Bot. Gaz. 144:439-449.
- LEHR, J. H. 1978. A catalog of the flora of Arizona. Northland Press, Flagstaff, AZ.
- and D. J. PINKAVA. 1980. A catalog of the flora of Arizona, Supplement I. J. Arizona-Nevada Acad. Sci. 15:19-32.
- MILLER, R. B. 1982. Hawkmoth pollination of *Aquilegia chrysantha* in southern Arizona. Bot. Soc. Amer. Misc. Publ. No. 162, p. 39.
- SCHAFFER, W. M. and M. V. SCHAFER. 1977. The reproductive biology of Agavaceae: I. Pollen and nectar production in four Arizona agaves. Southw. Naturalist 22:157-168.
- SHERBROOKE, W. C. and J. C. SCHEREENS. 1979. Ant-visited extrafloral (calyx and foliar) nectaries and nectar sugars of *Erythrina flabelliformis* Kearney in Arizona. Ann. Missouri Bot. Gard. 66:472-481.

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